Verh. Internat. Verein. Limnol.	27	64–73	Stuttgart, April 2000

Effects of natural light on nitrogen dynamics in diverse aquatic environments

Wayne S. Gardner, Peter J. Lavrentyev, Harvey A. Bootsma, Joann F. Cavaletto, Federico Troncone and James B. Cotner

Introduction

Solar radiation is a major force affecting the ecosystem dynamics of aquatic and terrestrial ecosystems. As the source of energy for photosynthesis, it allows plants to assimilate nutrients into energy-rich organic material at the base of food webs and provides energy for biogeochemical processes. The importance of the quality and quantity of light has been studied extensively in terms of its relationship to photosynthetic processes (e.g. KIRK 1994). The effect of light on nitrogen cycling in aquatic ecosystems has been less studied and has not been defined clearly, except for several studies of nutrient uptake as related to primary production processes (e.g. COCHLAN et al. 1991 and references cited therein). Light provides energy for photosynthesis and increases inorganic nutrient uptake, but excess light can also inhibit phytoplankton growth and nutrient uptake. These effects depend not only on the intensity of the light but also on its spectral characteristics and the physiology of component organisms.

The effects of light on heterotrophic nutrient regeneration processes are less apparent than are those for phytoplankton uptake processes because heterotrophic organisms do not usually depend on light for energy. For this reason, metabolic studies of heterotrophic aquatic organisms are usually conducted under dark conditions. However, light could affect biological nutrient regeneration mechanisms and rates in a variety of indirect ways. To develop an understanding of these effects, we must define the mechanisms of food web interactions and photochemical stimuli that may affect them. Additionally, ultraviolet light may affect nitrogen regeneration by photochemically converting dissolved organic nitrogen (or complexed inorganic forms) to ammonium or nitrate in surface waters (BUSHAW et al. 1996).

Research on microbial ecology over the past few decades has expanded our concepts of energy and nutrient transformations in aquatic ecosystems (POMEROY 1974, AZAM et al. 1983, SHERR et al. 1988). The current paradigm is that a large portion of the energy and nutrients fixed by primary producers in aquatic ecosystems passes through small organisms that constitute the "Microbial Food Web (MFW)". Details of this changing paradigm are still being defined for aquatic ecosystems. For example, small phytoplankton and bacteria are grazed by protists or microzooplankton, which are eaten by crustacean zooplankton or other metazoan invertebrates before the energy becomes available for higher trophic levels such as fish. With more trophic levels involved in energy and nutrient transformations, the relative quantity of fixed organic matter that is metabolically released as inorganic nutrients and carbon dioxide is increased (e.g. SUZUKI et al. 1996). If materials pass through the MFW before being incorporated into larger units of biomass, such as zooplankton, fixed nutrients will be recycled to a greater extent than if zooplankton or macrobenthos consume the phytoplankton directly. The community composition and trophic dynamics of autotrophic and heterotrophic organisms (e.g. HAGA et al. 1995, MILLER et al. 1995) and their responses to available light (LIPSCHULTZ et al. 1985) must therefore be studied to understand the effects of light on nutrient transformations and cycling rates in aquatic ecosystems.

Direct and indirect mechanisms for sunlight to affect nitrogen cycling rates and transformations in aquatic ecosystems could include the following.

Direct effects

Biotic

- Provide energy for photosynthesis, nutrient uptake, and/or N_2 fixation
- Increase algal metabolism and DON release
- UV cell damage and inhibition of nitrogen uptake
- Light inhibition of nitrification

0368-0770/00/0027-0064 $ 2.50

Abiotic

- Photochemical degradation of dissolved organic nitrogen (DON)
- Photochemical degradation of humic material with release of inorganic N

Indirect effects

- Increased supply rates of dissolved organic substrates through photosynthesis
- Photosynthetic production of O_2 that affects nutrient cycling processes
- Increased grazing due to increased production of primary producers
- Phytoplankton or zooplankton migration due to photoreception (biological pump)
- Light-induced metabolic activity or behavioral changes (e.g. respiration or grazing rate changes)

Questions

Rather than consider all of these potential effects in detail, we will examine patterns of ammonium uptake and regeneration in a variety of aquatic environments and make inferences about direct and indirect effects of light on nitrogen cycling dynamics in pelagic ecosystems. Specifically, we will focus on the following questions:

1. How does sunlight affect community uptake and regeneration rates of ammonium?
2. Does sunlight enhance DON release by phytoplankton?
3. Are effects of light on community regeneration rates related to microbial food web composition?

We discuss data from both freshwater and marine coastal systems because of the limited amount of data that are available from freshwater lakes. This approach is reasonable because salinity itself does not appear to be a major factor affecting biotic/light interactions.

Experimental approaches and site descriptions

Net concentration changes over time in light–dark experiments

Assuming that autotrophic processes occur in the presence of light, but not in the dark, and that heterotrophic processes occur both in the light and in the dark, we can gain insight into nutrient cycling mechanisms and rates by comparing nutrient concentration changes over time in light vs. dark bottles. We have conducted such experiments, in combination with organic (amino acids) and inorganic (ammonium) nutrient additions, to gain information about autotrophic and heterotrophic nutrient cycling processes as related to lower food web organisms.

Light/dark isotope dilution experiments with $^{15}NH_4^+$

Isotope dilution or enrichment experiments with ^{15}N tracers (e.g. $^{15}NH_4^+$ or ^{15}N-labeled amino acids) can provide information on nitrogen recycling rates under conditions of natural light and temperature. Isotope dilution experiments with added $^{15}NH_4^+$ assume that most regenerated ammonium is derived from ^{14}N-organic material whereas both isotopes of ammonium will be taken up in approximate proportion to their concentrations in the enriched solution (Blackburn 1979, Caperon et al. 1979). Conducting such experiments under both light/dark and dark conditions allows a direct assessment of the effects of light on community nitrogen cycling dynamics. However, the process of performing large numbers of such isotope experiments with dissolved $^{15}NH_4^+$ is quite challenging using mass analysis techniques. The need to distill or extract the ammonium from the water and convert it to N_2 before measurement of isotope ratios can be made by mass or emission spectrometry, requiring relatively large samples (e.g. >100 mL) for sufficient sensitivity and considerable time for sample processing. These constraints limit the number of samples that can be processed on ship or stored for later isolation and analysis.

We have developed an alternative direct-injection high performance liquid chromatographic technique to fractionate directly the two isotopic forms of ammonium in water (Gardner et al. 1995). This cation exchange fractionation is possible because a slightly larger proportion of the $^{15}NH_4^+$ than of the $^{14}NH_4^+$ occurs in the ionic form in the equilibrium reaction between ammonium and ammonia at pH values near a pK of about 9.0. The atom % of ^{15}N-NH_4^+ is determined by quantifying the retention-time shift in the sample ammonium peak relative to an internal ammonium standard under controlled chromatographic conditions. This method can be applied to relatively small water samples in environments where nutrient cycling rates are sufficient to allow measurement. It provides a convenient way to examine potential rates and processes under a variety of experimental conditions. We have used this approach to examine nitrogen cycling processes under light and dark conditions.

Site descriptions

As one of the Laurentian Great Lakes, Lake Michigan is a mesotrophic lake with many of the characteristics expected of a large temperate lake (Scavia & Fahnenstiel 1987). Phytoplankton are not normally limited by nitrogen in this lake, but examining nitro-

gen dynamics can provide insight into food web mechanisms relevant to nutrient and energy transformations that may be generalized to other aquatic systems. Our studies in Lake Michigan involved measuring net ammonium and amino acid concentration changes in light/dark substrate addition experiments and conducting $^{15}NH_4^+$ isotope dilution studies by tracer techniques, using mass spectrometry for isotope ratio determinations. The latter work was part of a larger study to examine the cycling of nitrogen through the various pool of nitrogen in the lake (BOOTSMA unpublished data).

The Mississippi River plume represents the region where the Mississippi River outflow enters the Gulf of Mexico both through the Southwest Pass of the Mississippi River mouth and, in addition, about 30% of the outflow of the Mississippi River enters the Gulf of Mexico via the Atchafalaya River and Bay located west of the Southwest Pass. The Mississippi River basin drains more than one-third of the USA mainland and thus delivers a large amount of nutrients into the Gulf of Mexico (ATWOOD et al. 1994). The plume is an example of an important region where massive quantities of nutrients from a turbid (low light) freshwater source are suddenly mixed with a low-nutrient environment with high light penetration. Primary production in the lower reach of the Mississippi River is low because of excessive turbidity, but primary and secondary production and associated processes peak at mid-salinity regions where abundant nutrients are combined with adequate light for high rates of primary production (LOHRENZ et al. 1988). This system provides an excellent example of a region where both nutrient and ecosystem dynamics are affected by the light environment.

Lake Maracaibo is a tropical, hypereutrophic lake in Venezuela on the northern tip of South America. At about 150 km long and 110 km wide, it is the largest lake in South America. It has a mean depth of 25 m and a maximum depth of 34 m (PARRI-PARDI 1983). This estuarine lake is connected to the Gulf of Venezuela via the Straits of Maracaibo and Bay El Tablazo and is brackish due to the intrusion of marine waters from the Straits to the hypolimnion of the lake. Primary productivity is very high in the lake with values as high as 3–8 g C m^{-2} day^{-1} reported for the northeastern area of the lake (SUTTON 1974). Lake Maracaibo receives large loads of nutrients from tributaries, sewage discharges, agricultural sources and, probably, the atmosphere. Despite large nutrient inputs and very high concentrations of ammonium in bottom waters (e.g. 70 µM NH_4^+-N L^{-1} in the center of the lake; unpublished data), Lake Maracaibo phytoplankton are considered to be limited by nitrogen (REDFIELD & EARLSTON DOE 1964).

Laguna Madre is a shallow, coastal lagoon along the Texas coast extending from Corpus Christi Bay to the Mexican border. Padre Island separates this lagoon from the Gulf of Mexico. The trophic status of the lagoon varies spatially and temporally depending on the amount of rainfall. Historically, most of Laguna Madre has been characterized as having healthy seagrasses, but, for the 7 year period of 1990 to 1997, the northern region had a continuous bloom of *Aureoumbra lagunensis,* "Texas Brown Tide", and displaced the sea grasses by making the water very turbid in some regions (BUSKEY et al. 1997). For example, Baffin Bay, which branches off the Laguna Madre south of Corpus Christi, was subjected to a particularly dense bloom of the brown tide during this period.

Results and discussion

1. How does light affect community uptake of ammonium?

Isotope dilution experiments in plastic bottles that eliminated UV light (i.e. polystyrene bottles incubated in a temperature-controlled, deck-top water bath in a blue plexiglass tank) showed enhanced ammonium uptake in the presence of natural light relative to dark bottles (e.g. Fig. 1 taken from GARDNER et al. 1997). Similar results from the literature are summarized by COCHLAN et al. (1991).

However, ultraviolet (280–400 nm) and photosynthetically available radiation (PAR = 400–700 nm) light can inhibit photosynthetic activity (see KIRK 1994) and nutrient uptake rates (COCHLAN et al. 1991). We investigated the effects of a variety of light conditions on potential uptake rates in Lake Maracaibo surface waters (GARDNER et al. 1998). Light conditions for surface samples included unshielded quartz tubes, screened polystyrene bottles (45% PAR reduction), screened (53% PAR reduction) or taped (dark) polypropylene syringes incubated in a deck-top incubator (open ice chest with overflowing lake water to maintain temperature) under full sun. Highest uptake rates were observed in the screened polypropylene syringes, followed by the dark syringes (Fig. 2). Light inhibition of uptake occurred in both the quartz and polystyrene bottles even though almost as much light passed through the polypropylene syringe as the polystyrene bot-

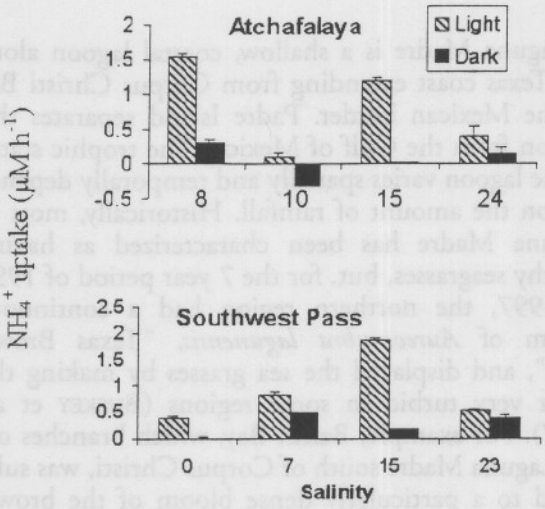

Fig. 1. Light and dark NH_4^+ uptake rates ($\mu M\ h^{-1}$) at Atchafalaya and Southwest Pass in the Mississippi River plume.

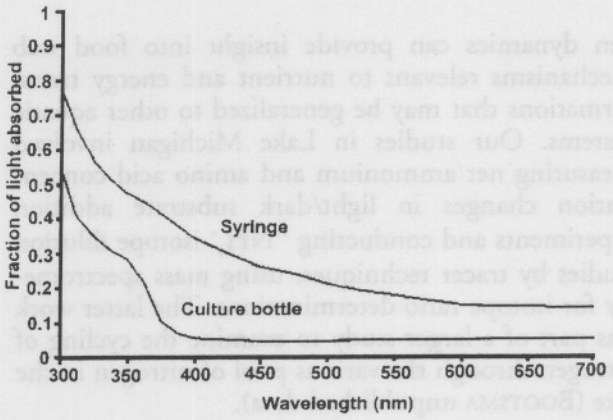

Fig. 3. Wavelength spectrum for fraction of light absorbed by container walls of polypropylene syringes and polystyrene culture bottles used for $^{15}NH_4^+$ isotope dilution experiments (taken from GARDNER et al. 1998).

tles. However, the light spectra varied considerably between the two types of plastic containers (Fig. 3 taken from GARDNER et al. 1998). Both plastic containers shielded much of the ultraviolet wavelengths, but the polystyrene did not block as much PAR as the polypropylene syringe. Thus, light inhibition may have been due, at least in part, to the visible part of the light spectrum. This conclusion is reasonable because the polypropylene container wall blocked some of the visible light that would normally be absorbed by phytoplankton (KIRK 1994).

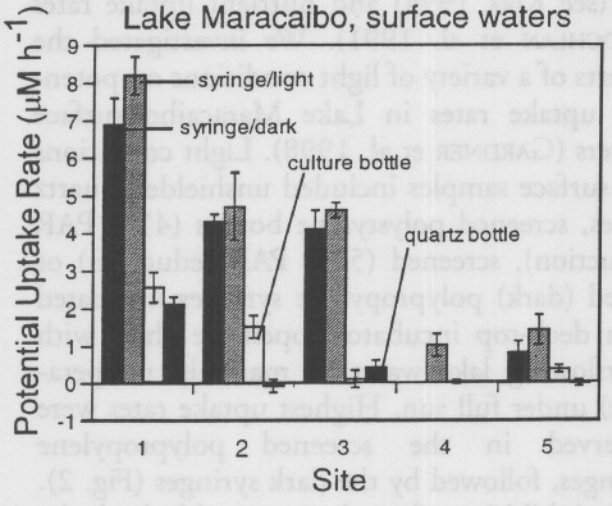

Fig. 2. Potential NH_4^+ uptake rates in Lake Maracaibo surface waters using different incubation vessels.

2. How does sunlight affect ammonium regeneration rates?

Abiotic nutrient regeneration. As mentioned above, a direct mechanism by which light may enhance ammonium regeneration rates is photochemical mineralization of DON with production of ammonium or nitrate (BUSHAW et al. 1996, MORAN & ZEPP 1997). This mechanism could be more important in systems containing N-rich DOM, as may be expected in hypereutrophic lakes such as Lake Maracaibo, but may be less important in systems containing DOM with a high C:N ratio. We conducted preliminary experiments in Lake Maracaibo on filtered (Rainin 0.2 µm nylon syringe filter) water incubated in quartz vessels. Measurable production and isotope dilution of ammonium was observed on sunny days compared to negligible production on one cloudy day (GARDNER et al. 1998). If we assume that the production was due to photochemical regeneration, the results indicate that up to 16–30% of the total ammonium regeneration could be contributed by photochemical breakdown of DON in surface waters. This value could be conservative because filtering the water before incubations may prevent normal production of DON by biotic mechanisms. On the other hand, such measurements likely overestimate the actual importance of photochemical regeneration because the sample was maintained artificially

at the water surface where ultraviolet effects would be maximized. In subsequent studies in the Laguna Madre, regeneration rate differences could not be distinguished between light and dark quartz bottles of filtered samples (unpublished data).

Biotic nitrogen regeneration. Intuitively, one would think that a heterotrophic process, such as biological ammonium regeneration in natural waters, would not be affected by the presence or absence of natural light. Based on this assumption, ammonium regeneration rates can be estimated by observing the accumulation of ammonium in dark bottles. We have used this approach in Lake Michigan to examine ammonium regeneration rates and to gain information about substrate limitation in the lake (e.g. GARDNER et al. 1987, 1989).

Several food web components can interact to cause a nutrient regeneration response to light. For example, WHEELER et al. (1989) observed that ammonium regeneration in the Pacific Ocean occurred exclusively at night, a result that was attributed to food web characteristics. Conversely, we have observed a positive effect of light on ammonium regeneration rates, as determined by isotope dilution, in a variety of aquatic environments when results from light/dark incubation vessels are compared to those from dark vessels under otherwise identical conditions. For example, consider the results from observations in the Mississippi River plume (Fig. 4 taken from GARDNER et al. 1997). In every paired comparison in this study, ammonium regeneration rates were higher under natural light conditions than in otherwise identical dark bottles. As a specific example of the concentration and isotope dilution differences, consider the changes in isotope dilution of $^{14}NH_4^+$ by looking at the changes in concentration and isotope ratio (atom % $^{15}NH_4^+$) and ammonium concentrations over time. Both ammonium concentration and atom % ^{15}N decreased much more in the light than in the dark (Fig. 5, taken from GARDNER et al. 1997) indicating that both ammonium uptake and regeneration were enhanced by the presence of visible light.

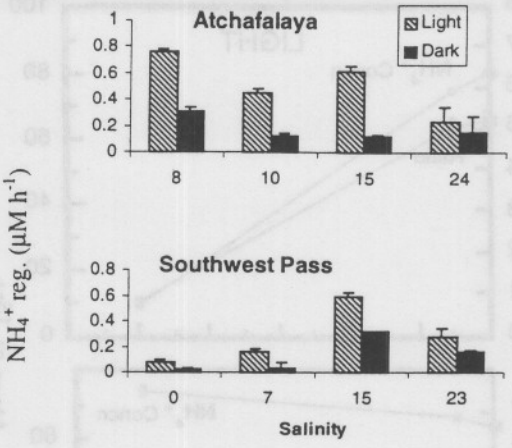

Fig. 4. Light and dark NH_4^+ regeneration rates ($\mu M\ h^{-1}$) at Atchafalaya and Southwest Pass in the Mississippi River plume.

These results were obtained with relatively high level additions of $^{15}NH_4^+$, but, interestingly, even more striking results were observed in Lake Michigan with tracer-level additions of $^{15}NH_4^+$ in relatively cold waters (Fig. 6). Thus, the pattern of light/dark differences in regeneration rates was similar in the Mississippi River plume and Lake Michigan, even though environmental conditions and analytical approaches used to examine the two systems were quite different.

Why were ammonium regeneration rates higher in the light than in the dark for identical sub-samples incubated identically over the same time intervals? Hypothesized reasons for these light-dependent differences in ammonium regeneration rates are: (1) increased release rates of labile DON compounds (e.g. amino acids) coupled with rapid microbial remineralization, (2) increased growth and grazing loses of small phytoplankton, or (3) modified activity or behavior of the grazing organisms, such as protists, responsible for ammonium regeneration in the water column. These and other processes may be occurring simultaneously and interactively.

3. Is light-driven DON release by phytoplankton important to pelagic nitrogen cycling?

Recent evidence suggests that release of DON compounds, such as dissolved free amino acids,

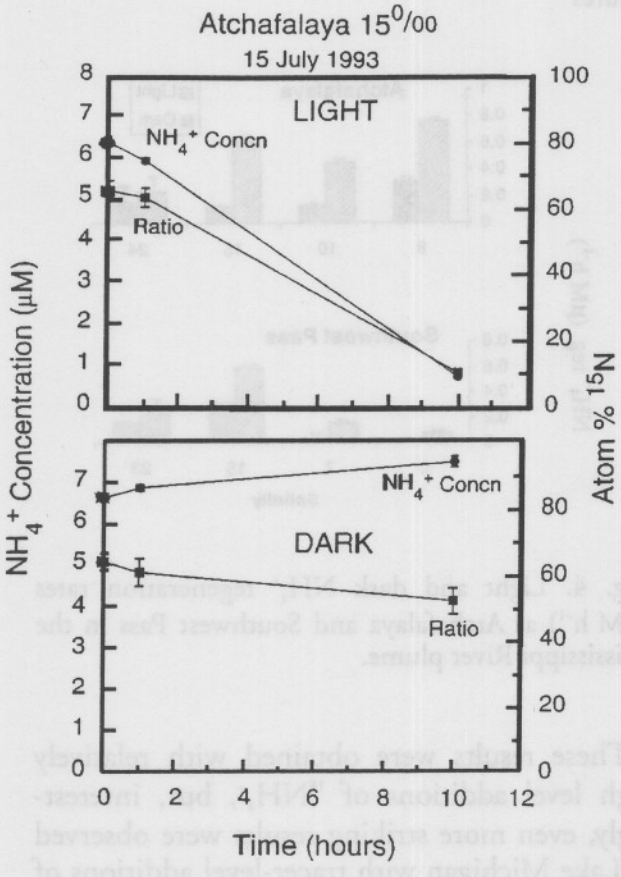

Fig. 5. Light and dark NH_4^+ concentration and isotope ratio (atom % ^{15}N) vs. incubation time at Atchafalaya in the Mississippi River plume.

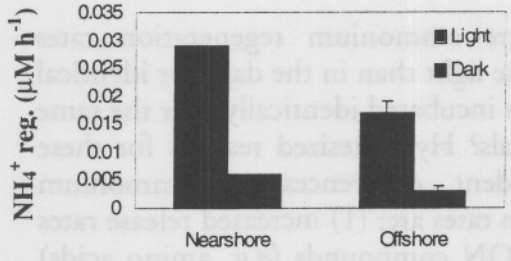

Fig. 6. Light and dark NH_4^+ regeneration ($\mu M\ h^{-1}$) Lake Michigan at nearshore and offshore sites.

by phytoplankton may be a major process for nitrogen cycling in aquatic ecosystems (Bronk & Glibert 1991, Cotner & Gardner 1993, Bronk et al. 1994, Fuhrman 1990). Although this potentially light-driven process appears to be important, it is difficult to assess in nature because of the rapid turnover rates of highly labile compounds such as amino acids. One approach that we have used to examine potential release rates for amino acids is to add sufficient levels of amino acids to "saturate" bacterial uptake sites, and then observe differences in net amino acid uptake rates in light vs. dark bottles. If concentrations of added amino acids are reduced more slowly in the light than in the dark, these differences in removal rates can be interpreted as representing amino acids (primary amines) that are released by metabolizing phytoplankton, assuming that light and dark bacterial uptake rates are the same. A linear relationship between these apparent amino acid release rates and dark ammonium accumulation rates in similar unfortified water samples (Gardner et al. 1987) is consistent with the idea that amino acid release by phytoplankton could be an important process for ammonium regeneration by microbial food web organisms. Comparison of amino acid turnover rate patterns with ammonium regeneration rates across a salinity gradient in the Mississippi River plume showed almost identical patterns for the two processes (Fig. 7 taken from Cotner & Gardner 1993).

To gain more insight into the interactions of ammonium and dissolved free amino acids (DFAA) with labile high molecular weight dissolved organic carbon (HMW DOC; Amon & Benner 1994) under light vs. dark conditions, we conducted experiments involving addition of these materials to water samples containing natural biota in the Mississippi River plume (Gardner et al. 1996). The HMW DOC is labile and has relatively high C:N ratios (e.g. C:N of about 14–20; personal communication, R. Benner, University of Texas Marine Science Institute) relative to that for amino acids (C:N of about 5). Concentration trends of ammonium and amino acids and changes in atom % ^{15}N-NH_4^+ over time in both light and dark bottles, with and without the addition of HMW DOM, were observed over time. Thus, potential interactions of light, HMW DOM, nitrogen (inorganic and organic), and natural biota were observed in these samples (Gardner et al. 1996).

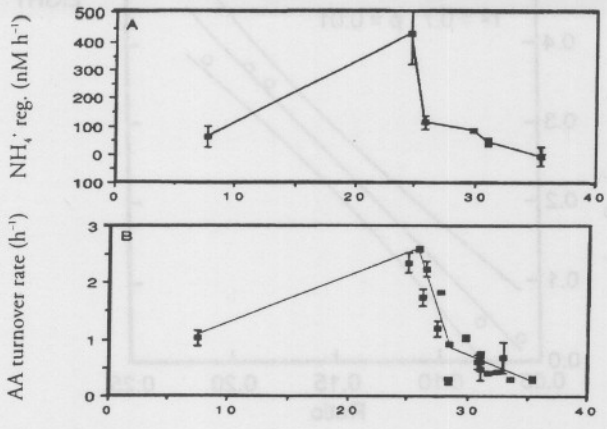

Fig. 7. NH_4^+ regeneration (nM h^{-1}) (A) and amino acid turnover rates (h^{-1}) (B) in the Mississippi River plume.

Amino acids were removed at comparable rates in the light and dark but removal rates were much higher in the presence of added HMW DOM than in the controls without the additions (GARDNER et al. 1996), as expected for heterotrophic uptake. The high rate of amino acid uptake, particularly in the presence of HMW DOM, suggests that the natural populations of bacteria were accustomed to assimilating amino acids at high rates even though ambient concentrations were very low. An explanation could be rapid turnover of amino acids in this enriched mid-plume environment. If labile DOM with a high C:N ratio is available to support metabolic energy requirements, the bacteria may be able to use that energy to assimilate available N (ammonium or amino acids) into biomass. Conversely, ammonium is regenerated more efficiently when amino acids (or other compounds with low C:N ratios) predominate. Bacterial growth rates were high in all bottles with added amino acids but were stimulated even further by the addition of HMW DOM. Additionally, they were high in the light sample with added HMW DOC and ammonium, but not in the comparable dark sample. These results suggest that, in the presence of light, labile organic nitrogen may be cycled in the form of small compounds such as amino acids that can be incorporated into microbial biomass or remineralized (GARDNER et al. 1997).

4. Are the effects of light on community regeneration rates related to microbial food web composition?

Comparison of light and dark bottle results in Lake Maracaibo indicated that ammonium regeneration rates were usually higher in the light than in the dark but that the differences were not significant. This lack of significance in comparison of light/dark regeneration rates may have been related to the fact that phytoplankton are nitrogen limited in Lake Maracaibo despite the hypereutrophic status of the lake. Light/dark differences in phytoplankton uptake rates tend to be less pronounced in nitrogen-starved than in nitrogen-replete phytoplankton (COCHLAN et al. 1991). However, ammonium regeneration rates under approximately normal light conditions were related to the carbon-based ratio of heterotrophic nanoflagellate (HNAN) to bacteria ($r^2 = 0.58$, $P < 0.01$; Fig. 8) that may reflect the degree of bacterivory. This interesting result suggests that ammonium regeneration rates may be related directly to bacterivory in Lake Maracaibo (GARDNER et al. 1998). However, dark bottles from the same sites did not show a significant correlation between ammonium regeneration and the HNAN:bacterial carbon ratio, possibly due to different feeding behavior in the dark.

A similar comparison in Laguna Madre also showed a highly significant relationship between ammonium regeneration rates and the HNAN:bacterial carbon ratio under natural light conditions ($r^2 = 0.7$, $P < 0.01$), but again there was no significant relationship between these variables for identical samples incubated in the dark ($r^2 = 0.06$, $P = 0.63$; Fig. 9). An intriguing observation from this statistically significant comparison under natural light was that the two lowest values, for both ammonium regeneration rates and the HNAN:bacteria ratios, were observed at sites with opposite trophic characteristics. One of these sites was the hypereutrophic Baffin Bay, which was experiencing a dense algal bloom of Texas Brown Tide (>200,000 cells/mL) at the time of sampling, whereas the other was a heterotrophically dominated oligotrophic site overlying a sea

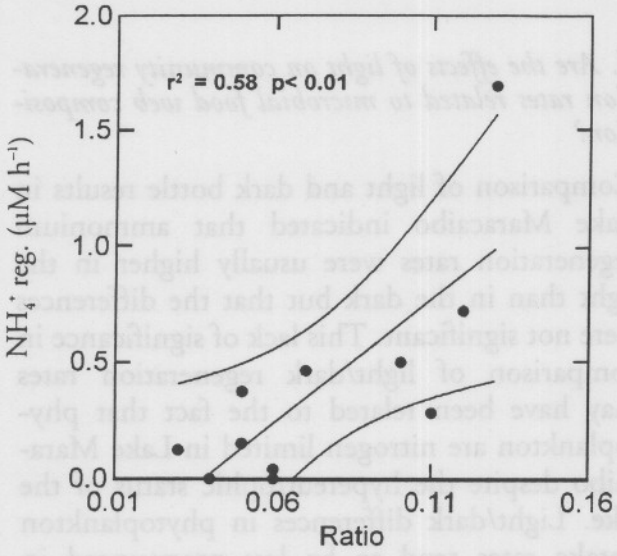

Fig. 8. NH_4^+ regeneration rates (µM h^{-1}) vs. HNAN:bacteria in Lake Maracaibo under ca. natural light conditions.

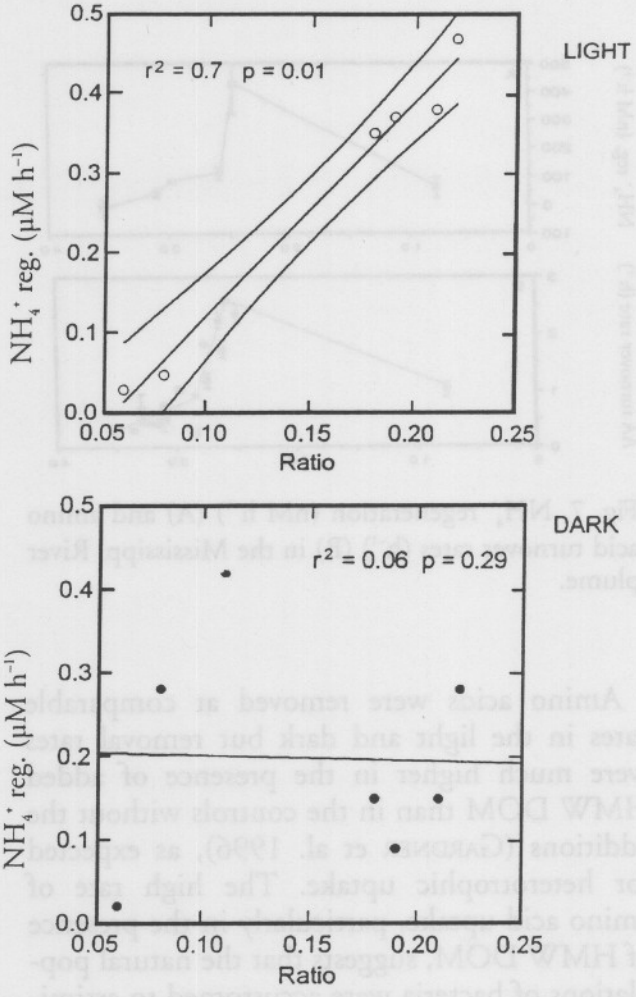

Fig. 9. Light and dark NH_4^+ regeneration (µM h^{-1}) vs. HNAN:bacteria in Laguna Madre.

grass bed in the lower Laguna Madre (personal communication, SUSAN ZIEGLER, University of Texas Marine Science Institute). Furthermore, except for the sample from the oligotrophic lower Laguna Madre station that was incubated for about 4 h, all of these incubations were done over intervals of about 1 h. The difference, in the predictability of ammonium regeneration rate patterns relative to the HNAN:bacterial carbon ratios, between light and dark incubations was surprising. The short incubation intervals (generally 1 h) for the Laguna Madre experiments, relative to expected organism turnover times, may argue against the notion that enhanced release of DON by phytoplankton, followed by the uptake and recycling of the DON by microbial food web organisms, was the major cause for this short-term light-mediated result. An alternative explanation may be a modified behavior of the HNAN in response to light. This possible relationship offers a logical reason to study possible photoreception by heterotrophic components of microbial food webs in aquatic ecosystems.

Conclusions

1. Sunlight can affect ammonium regeneration rates, as well as uptake rates, in near-surface waters.
2. The major mechanism appears to be microbial food web process changes in response to light.

Research recommendations

1. Consider light as a factor influencing nutrient regeneration rates in aquatic ecosystems.
2. Conduct heterotrophic process experiments under natural light as well as dark conditions.
3. Consider microbial food web-light interactions in conceptual models of nutrient dynamics.
4. Quantify specific food web mechanisms responsible for light-related nutrient cycling phenomena (e.g. DON release by phytoplankton, photoreception by heterotrophic organisms, vertical migration).

Acknowledgements

We thank MARK MCCARTHY for technical and edito-

rial assistance, ED BUSKEY for providing ship time on the R/V Longhorn in the Laguna Madre and Baffin Bay, and MICHAEL ARTS for a careful review of the manuscript. The Nancy Lee and Perry Bass Chair Endowment to The University of Texas Marine Science Institute supported manuscript preparation.

References

AMON, R. M. W. & BENNER, R., 1994: Rapid cycling of high molecular weight dissolved organic matter in the ocean. – *Nature* **369**: 549–552.

ATWOOD, D. K., BRATKOVICH, A., GALLACHER, M. & HITCHCOCK, G. L., 1994: Introduction to the dedicated issue of papers from NOAA's Nutrient Enhanced Coastal Ocean Productivity Study. – *Estuaries* **17**: 729–731.

AZAM, F. et al., 1983: The ecological role of water-column microbes in the sea. – *Mar. Ecol. Prog. Ser.* **10**: 257–263.

BLACKBURN, H. T., 1979: Method for measuring rates of NH_4^+ turnover in anoxic marine sediments, using a ^{15}N–NH_4^+ dilution technique. – *Appl. Environ. Microbiol.* **37**: 760–765.

BRONK, D. A., & GLIBERT, P. M., 1991: A ^{15}N-tracer method for the measurement of dissolved organic nitrogen release by phytoplankton. – *Mar. Ecol. Prog. Ser.* **77**: 171–182.

BRONK, D. A., GLIBERT, P. M. & WARD, B. B., 1994: Nitrogen uptake, dissolved organic nitrogen release, and new production. – *Science* **265**: 1843–1846.

BUSHAW, K. L. et al., 1996: Photochemical release of biologically available nitrogen from aquatic dissolved organic matter. – *Nature* **381**: 404–407.

BUSKEY, E. J., MONTAGNA, P. A., AMOS, A. F. & WHITLEDGE, T. E., 1997: Disruption of grazer populations as a contributing factor to the initiation of the Texas brown tide algal bloom. – *Limnol. Oceanogr.* **42**: 1215–1222.

CAPERON, J., SCHELL, D., HIROTA, J. & LAWS, E., 1979: Ammonium excretion rates in Kaneohe Bay, Hawaii, measured by a ^{15}N-isotope dilution technique. – *Mar. Biol.* **54**: 33–40.

COCHLAN, W. P., PRICE, N. M. & HARRISON, P. J., 1991: Effects of irradiance on nitrogen uptake by phytoplankton: comparison of frontal & stratified communities. – *Mar. Ecol. Prog. Ser.* **69**: 103–116.

COTNER, J. B., & GARDNER, W. S., 1993: Heterotrophic bacterial mediation of ammonium and dissolved free amino acid fluxes in the Mississippi River plume. – *Mar. Ecol. Prog. Ser.* **93**: 75–87.

FUHRMAN, J. A., 1990: Dissolved free amino acid cycling in an estuarine outflow plume. – *Mar. Ecol. Prog. Ser.* **66**: 197–203.

GARDNER, W. S., CHANDLER, J. F., LAIRD, G. A. & CARRICK, H. J., 1987: Sources and fate of dissolved free amino acids in epilimnetic Lake Michigan water. – *Limnol. Oceanogr.* **32**: 1353–1362.

GARDNER, W. S., CHANDLER, J. F. & LAIRD, G. A. 1989: Organic mineralization and substrate limitation of bacteria in lake Michigan. – *Limnol. Oceanogr.* **34**: 478–485.

GARDNER, W. S., BOOTSMA, H. A., EVANS, C. & ST. JOHN, P. A., 1995: Improved chromatographic analysis of ^{15}N:^{14}N ratios in ammonium or nitrate for isotope addition experiments. – *Mar. Chem.* **48**: 271–282.

GARDNER, W. S. et al., 1996: Effects of high molecular weight dissolved organic matter on nitrogen dynamics in the Mississippi River plume. – *Mar. Ecol. Prog. Ser.* **133**: 287–297.

GARDNER, W. S., CAVALETTO, J. F., COTNER, J. B. & JOHNSON, J. R., 1997: Effects of natural light on nitrogen cycling rates in the Mississippi River plume. – *Limnol. Oceanogr.* **42**: 273–281.

GARDNER, W. S. et al., 1998: Nitrogen cycling rates & light effects in tropical Lake Maracaibo, Venezuela. – *Limnol. Oceanogr.* **43**: 1814–1825.

HAGA, H., NAGATAW, T. & SAKAMOTO, M., 1995: Size fractionated NH_4^+ regeneration in the pelagic environments of two mesotrophic lakes. – *Limnol. Oceanogr.* **40**: 1091–1099.

KIRK, J. T. O., 1994: *Light and Photosynthesis in Aquatic Ecosystems.* – Cambridge. 509 pp.

LIPSCHULTZ, F., WOFSY, S. C. & FOX, L. E., 1985: The effects of light and nutrients on rates of ammonium transformation in a eutrophic river. – *Mar. Chem.* **16**: 329–341.

LOHRENZ, S. E. et al., 1988: Interrelationships among primary production, chlorophyll, & environmental conditions in frontal regions of the western Mediterranean Sea. – *Deep Sea Res.* **35**: 793–810.

MILLER, C. A., PENRY, D. L. & GLIBERT, P. M., 1995: The impact of trophic interactions on rates of nitrogen regeneration and grazing in Chesapeake Bay. *Limnol. Oceanogr.* **40**: 1005–1011.

MORAN, M. A., & ZEPP, R. G., 1997: Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. – *Limnol. Oceanogr.* **42**: 1307–1306.

PARRI-PARDI, G., 1983: Cone-shaped hypolimnion and local reactor as outstanding features in eutrophication of Lake Maracaibo. – *J. Great Lakes Res.* **9**: 439–451.

POMEROY, L. R., 1974: The ocean's food web, a changing paradigm. – *Bioscience* **24**: 499–504.

REDFIELD, A. C. & EARLSTON DOE, L. A., 1964: Lake Maracaibo. – *Verh. Internat. Verein. Limnol.* **15**: 100–111.

SCAVIA, D., & FAHNENSTIEL, G. L., 1987: Dynamics of Lake Michigan phytoplankton: mechanisms controlling epilimnetic communities. – *J. Great Lakes Res.* **13**: 103–120.

SHERR, B. F., SHERR, E. B. & HOPKINSON, C. S., 1988: Trophic interactions within pelagic microbial communities: Indications of feedback regulation of carbon flow. – *Hydrobiologia* **159**: 19–26.

SUTTON, E. A., 1974: Study of effects of oil discharges & domestic & industrial wastewaters on the fisheries of Lake Maracaibo, Venezuela. – In: TEMPLETON, W. L. (ed.): *Ecological Characterization and Domestic and Industrial Wastes.* – Battelle Pacific Northwest Laboratories, Richland, Washington.

SUZUKI, M., SHERR, E. B. & SHERR, B. F., 1996: Estimation of ammonium regeneration efficiencies associated with bacte-

rivory in pelagic food webs via a ^{15}N-tracer method. – *J. Plankton Res.* 18: 411–428.

WHEELER, P. A., KIRCHMAN, D. L., LANDRY, M. R. & KOKKINAKIS, S. A. 1989: Diel periodicity in ammonium uptake and regeneration in the oceanic subarctic Pacific: Implications for interactions in microbial foodwebs. – *Limnol. Oceanogr.* 34: 1025–1033.

Authors' addresses:

W. S. GARDNER, P. J. LAVRENTYEV, University of Texas Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78373, USA.

H. A. BOOTSMA, SADC/GEF Lake Malawi / Nyasa Biodiversity Conservation Project, P.O. Box 311, Salima, Malawi.

J. F. CAVALETTO, NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA.

F. TRONCONE, Instituto para el Control y la Conservacion de la Cuenca del Lago Maracaibo (ICLAM), Maracaibo, Estado Zulia, Venezuela.

J. B. COTNER, Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108, USA.